Reference: *Biol. Bull.*, **154**: 226–240. (April, 1978)

ANTENNULAR CHEMOSENSITIVITY IN THE SPINY LOBSTER, *PANULIRUS ARGUS*: STUDIES OF TAURINE SENSITIVE RECEPTORS [1]

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A recent study of the antennular chemosensory system in *Panulirus argus* showed that the low molecular weight fractions of extracts of several potential food organisms duplicated the receptor activity elicited by the total unfractionated extracts (Ache, Fuzessery and Carr, 1976). Further, in at least one of the above extracts, the amino acids were shown to account for a large portion of the activity with taurine being the single most stimulatory amino acid (Johnson and Ache, 1978). Taurine emerges as an effective stimulant in other crustacean studies as well (Case, 1964; Crisp, 1967; Ache, 1972; Shepheard, 1974; Carr and Gurin, 1975; Fuzessery and Childress, 1975; Allison and Dorsett, 1977). Taurine sensitive receptors, with response thresholds as low as 10^{-10} M, occur on both the lateral and medial antennular filaments of the spiny lobster (Fuzessery, in preparation). The present study examines the molecular specificity of taurine sensitive receptors by comparing the stimulatory capacity of taurine with that of taurine analogs, derivatives, and structurally related compounds. The results indicate that antennular taurine receptors of *P. argus* are characterized by a narrow and consistent specificity similar to that of the taurine endoreceptors of diverse organisms.

Materials and Methods

Excised antennular filaments were fitted with a Sylgard sleeve over their proximal end, and inserted into a tubular stimulating chamber. The sleeve separated fluid in the stimulating chamber from a second compartment containing about 10 ml of *Panulirus* saline (Mulloney and Selverston, 1974) into which the filament's proximal end projected. The preparation was perfused with oxygenated *Panulirus* saline introduced under pressure through a tapered glass capillary inserted in the cut distal tip of the filament. Axons were exposed for recording by cutting the articular membrane between the fourth and fifth most proximal segments of the filament and removing the cuticle in the manner of removing insulation from a wire. Care was taken to place minimal stress on the axon bundle during this process. Receptor activity was recorded extracellularly using a monopolar plati-

[1] This study was supported in part by NSF Grant No. PCM-73-07076 A02 (WESC) and a grant from the Whitehall Foundation (BWA).

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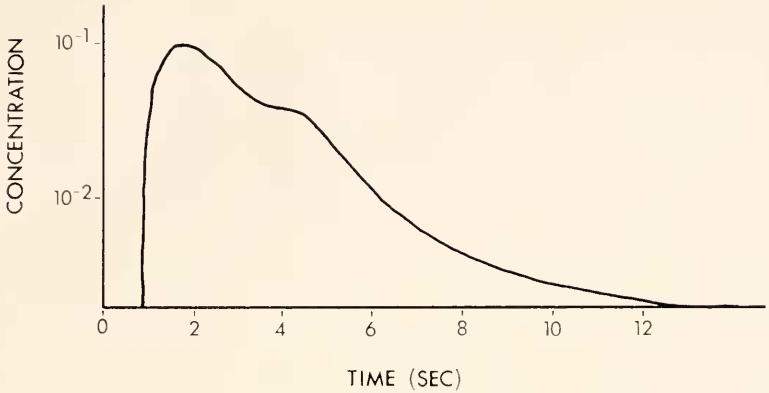

FIGURE 1. Temporal profile of 50-μl stimulant pulse as monitored by densitometry.

num-iridium hook electrode referenced against an Ag-AgCl pellet submerged in the 10 ml saline bath. Signal amplification and display involved standard electrophysiological instrumentation. All activity was stored on magnetic tape for subsequent analysis.

Reagent-grade artificial sea water (ASW, MBL formula) continuously entered the stimulating chamber at the filament's proximal end and flowed distally over the filament at a rate of 10 ml/min. Fifty-microliter pulses of test stimulant were pipetted into this carrier flow of ASW through a port 2 cm upstream from the preparation. Figure 1 shows the temporal profile of a stimulus pulse, measured by monitoring a pulse of methylene blue with a densitometer located at the midpoint of the tubular compartment.

All compounds employed in the study were obtained from commercial sources and used to prepare 10^{-4} M stock solutions in ASW. These were frozen until needed, thawed and serially diluted with ASW to the required test concentrations. All solutions were tested at the pH (7.5) and temperature (*ca.* 22° C) of the carrier ASW flow.

The general protocol in each experiment was to search for single taurine sensitive neurons while stimulating with 10^{-5} M taurine. Nerve bundles containing taurine sensitive units were sub-divided until only the taurine sensitive unit remained, or the taurine sensitive unit could be clearly discriminated from background multiunit activity. Single units were identified as such by consistent amplitude, configuration, regularity of interspike interval and relative response latency. Unless otherwise indicated, the entire group of compounds tested in an experiment was applied to each taurine sensitive receptor. Taurine was applied at the beginning, midpoint and end of each test series. Any loss of activity in response to the final taurine application voided that test series. The application sequence of test compounds was randomized. A 30-sec period followed the introduction of each test solution, during which time the filament was flushed vigorously with two 1-ml injections of ASW. Preliminary trials indicated 30 sec was sufficient time for full receptor recovery at the stimulant concentrations used. Procedural details unique to specific experiments are included in Results.

Response parameters of maximum impulse frequency, number of impulses/response and response duration were quantified by playing taped responses through a window discriminator and electronic counter (Haer 7400 series). The transformed output was displayed on a storage oscilloscope in the form of a post-stimulus time histogram of the impulses/100 msec over the duration of the response. Maximum impulse frequency was determined by observing the greatest number of impulses collected in a single 100 msec time interval. The number of impulses/response was determined as the sum of the impulses in all time intervals over the duration of the response. The index of relative stimulatory capacity (RSC) used in this study to compare stimulants was calculated as the number of impulses/response elicited by a given compound divided by the number of impulses/response elicited by taurine × 100. Hence, the RSC value for taurine on each receptor is 100. In a few cases where chemoreceptors were spontaneously active, an index of average baseline activity in the absence of chemical stimulation was calculated and subtracted from the activity elicited by test compounds in that individual receptor.

Results

Preliminary tests of taurine—dose/response relationships

Taurine was tested over a concentration range of 10^{-11} to 10^{-4} M on 18 lateral and 18 medial filament receptors. The average values for maximum impulse frequency, impulses/response and response duration are shown in Figure 2. Maxi-

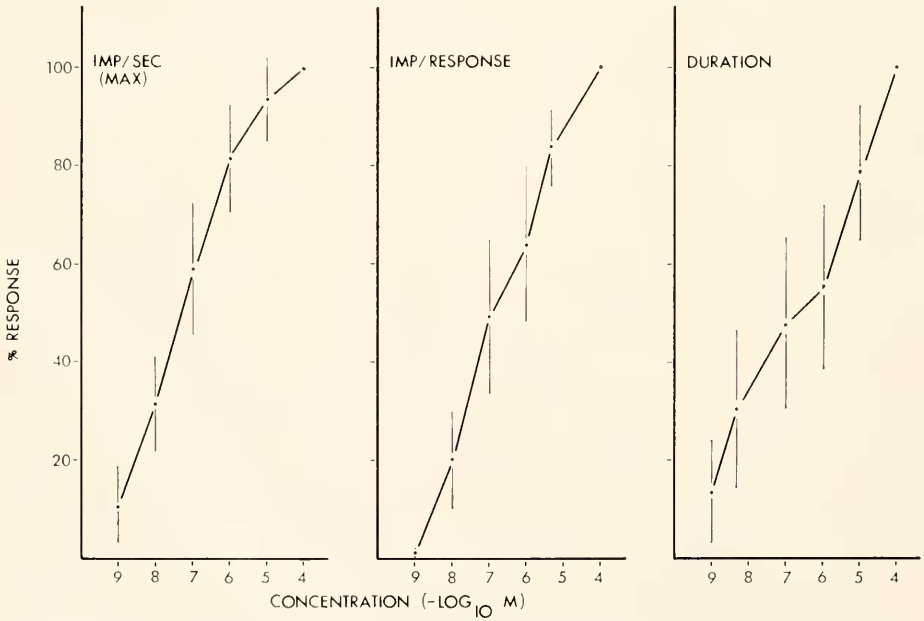

Figure 2. Average dose/response relationships given by 36 antennular receptors to taurine stimulation. Ordinate indicates percentage of maximum response, *i.e.*, that to 10^{-4} M taurine.

TABLE I

Relative stimulatory capacity (RSC) of eight taurine analogs and derivatives tested on 21 taurine sensitive receptors. All compounds were tested at 10^{-5} M. Value of taurine response is an arbitrary 100 in all cases. Blanks indicate no response. RSC values are based on total impulses/response.

Compound	Receptor number																				$\bar{X}$*	s.d.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21		
β-Alanine	66	82	49	49	67	14	14	36	47	40	55	59	73	57	5	79	47	43	80	94	46	52	±23
Hypotaurine	56	82	71	51	17	3	15	26	40	52	46	44	38	30	5	71	46	41	74	72	25	43	±23
2-Aminoethyl phosphonic acid																				43		2	± 9
Aminomethyl sulfonic acid																11	21	45				4	±10
Cysteic acid																13			10			1	± 3
Hydroxyethane sulfonic acid																				25	12	2	± 6
Ethane sulfonic acid																			14			1	± 3
2-Chloroethane sulfonic acid																						0	

* $\bar{X}$ = average RSC value. For individual receptors, an RSC value of zero was recorded when there was no response to a compound.

mum impulse frequency began to plateau at concentrations of 10^{-5} and 10^{-4} M, while the total number of impulses and the response duration increased regularly over the entire concentration range. The large standard deviations of each parameter reflect in part variations in sensitivity among receptors. Individual threshold concentrations ranged from 10^{-8} to 10^{-10} M. As subsequent data will indicate these deviations also reflect variations in the slopes of the dose/response curves that are characteristic of individual receptors. Based on these findings, a standard test concentration of 10^{-5} M taurine was chosen to insure a strong yet nonsaturating response from all receptors.

Specificity of taurine sensitive receptors

The stimulatory capacity of taurine (= 2-aminoethyl sulfonic acid) was compared with that of three analogs and five related sulfonic acids. All compounds were tested at 10^{-5} M on each of 21 taurine sensitive receptors on the lateral and medial filaments. Calculations of the relative stimulatory capacity (RSC) for each compound on each receptor are summarized in Table I. A comparison of the RSC values reveals that only taurine and its carboxylic and sulfinic acid analogs, β-alanine and hypotaurine, stimulated all receptors.

Other comments on data in Table I are presented below following the presentation of some additional results.

To further define response specificity, thirteen additional compounds, structurally-related to taurine, were tested at 10^{-5} M on each of 18 taurine sensitive lateral- and medial-filament receptors. The resulting RSC values are presented in Table II. Structural formulae of compounds that were tested are shown in Figure 3. Conclusions concerning receptor specificity are summarized below.

1. Compounds with one terminal basic group and one terminal acidic group separated by two carbon atoms were most effective. Taurine and its analogs, hypotaurine, β-alanine and 2-aminoethyl-phosphonic acid all meet these structural requirements. Though less stimulatory than taurine, the analogs hypotaurine and β-alanine stimulated all receptors and their RSC values with individual receptors were consistently similar. The phosphonic acid analog was dramatically less effective and elicited a response from only one of the 21 receptors tested (Table I).

2. Compounds with one terminal basic group and one terminal acidic group separated by more than two carbon atoms were also effective although the RSC values decreased with the distance of separation of the charged groups. This is illustrated in Table II by comparing the RSC values of the following: β-alanine > γ-amino-n-butyric acid (GABA) > 5-aminovaleric acid > 6-aminocaproic acid. Note also that two isomers of GABA, 2-aminobutyric acid and 3-aminobutyric acid, with nonterminal amine groups, are markedly less effective than GABA.

3. Compounds with a terminal basic group and a terminal acidic group separated by only one carbon atom (rather than two carbon atoms) were markedly less effective. This is shown in Table I by the low incidence of receptor stimulation and the low RSC value of aminomethyl sulfonic acid (AMS). Note that AMS, like taurine, has terminal amine and sulfonic acid groups. Later in the report data are presented to show that the AMS analog, glycine, as well as other α-amino acids are virtually ineffective in taurine sensitive receptors.

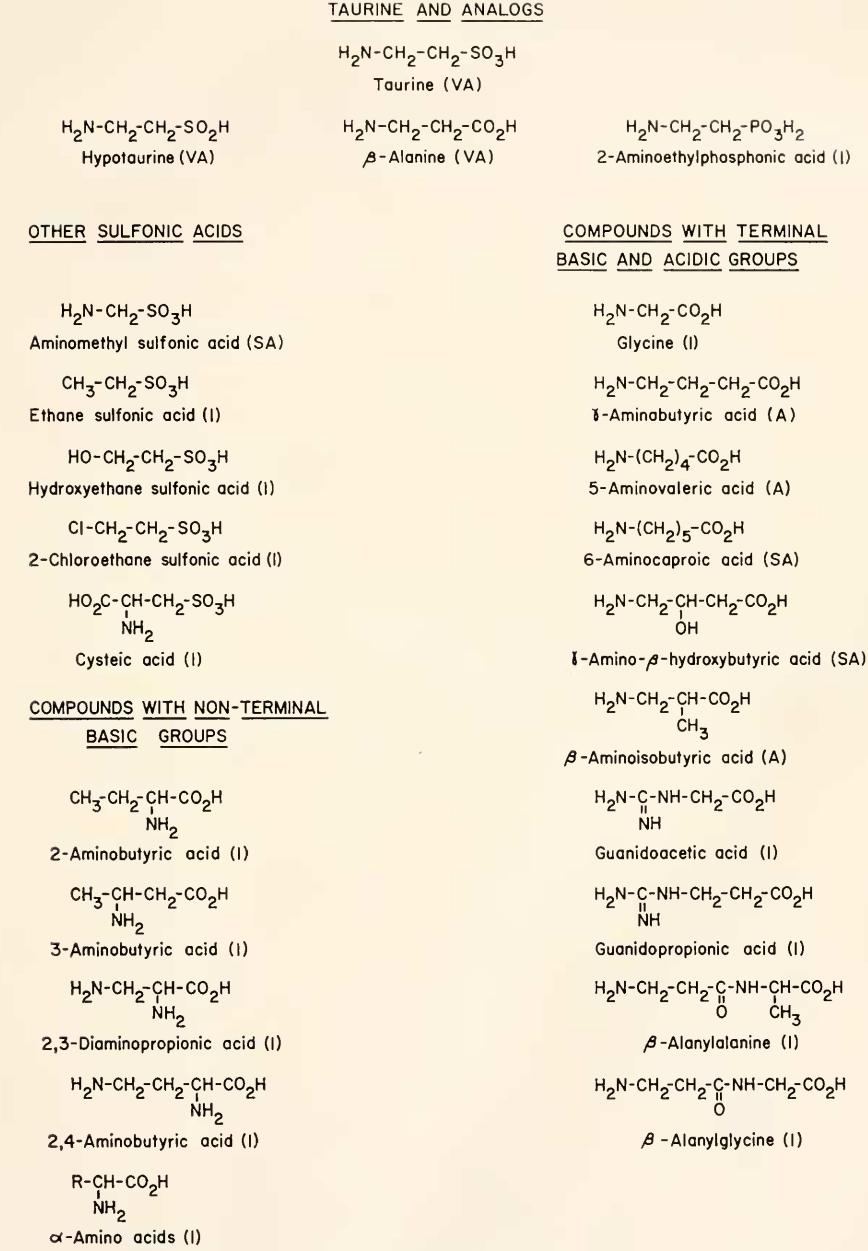

FIGURE 3. Structural formulae of compounds tested on taurine sensitive receptors. Indices of relative activity are as follows: (VA), very active; (A), active; (SA), slightly active; (I), virtually inactive.

TABLE II

Relative stimulatory capacity (RSC) of 16 compounds structurally-related to taurine tested on 18 taurine sensitive receptors. All compounds were tested at 10^{-5} M. Value to taurine is an arbitrary 100 in all cases. Blanks indicate no response. RSC values are based on total impulses/response.

Compound	Receptor number																		$\bar{X}$*	s.d.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18		
Hypotaurine	76	88	38	82	53	30	99	58	41	50	63	73	70	56	77	89	54	32	63	±20
β-Alanine	43	67	48	82	27	45	76	71	59	44	51	64	74	64	79	81	63	29	59	±17
γ-Amino-n-butyric acid (GABA)						8	4	12	12		5	27	28	29	30	21	32	19	13	±12
β-Aminoisobutyric acid										3	5	10	12	9	24	13	63	12	8	±15
5-Aminovaleric acid												10	18	8	20	19	25	17	7	± 9
DL-γ-Amino-β-hydroxybutyric acid												5	12	5	10	9	16	10	4	± 5
6-Aminocaproic acid													18	1	3	7	21	10	3	± 7
Guanidoacetic acid															8		17	6	2	± 4
DL-3-Amino butyric acid															6	9		6	1	± 3
β-Guanidopropionic acid																	19	15	2	± 6
DL-2-Aminobutyric acid																		1		
Glycylglycine																		1		
β-Alanylalanine																		1		
β-Alanylglycine																		1		
2,3-Diamino-propionic acid																		1		
2,4-Aminobutyric acid																		1		

* $\bar{X}$ = average RSC value, see footnote to Table I.

4. Taurine derivatives lacking the basic amine group were markedly less effective. This is shown by the low incidence of receptor stimulation and the low RSC values of ethane sulfonic acid, hydroxyethane sulfonic acid and chloroethane sulfonic acid (Table I).

5. The addition of a neutral side chain decreased the effectiveness of a compound. γ-Amino-β-hydroxybutyric acid differs from GABA by having a hydroxyl group and yet has a much lower RSC value (Table II). Likewise, β-aminoisobutyric acid differs from β-alanine by having a methyl group and yet has a much lower RSC value.

6. Compounds with an *alpha*-amine group in addition to a terminal amine group were virtually ineffective. Note in Table II that 2,3-diaminoproprionic acid and 2,4-aminobutyric acid are virtually inactive, whereas the closely related compounds, β-alanine and GABA, have marked activities.

7. Compounds in which the terminal basic group is a guanido group rather than an amine group were far less effective. This is shown in Table II by the very low RSC values of guanidoacetic and β-guanidopropionic acid.

8. Two dipeptides containing the stimulatory amino acid β-alanine were ineffective thereby suggesting that activity is lost when the carboxyl group is involved in a peptide bond (Table II). Likewise, the presence of two acidic groups apparently negates activity as shown by the ineffectiveness of cysteic acid (Table I).

The data in Table II also indicate the existence of a distinct relationship between the average RSC value of a compound and the number of receptors responding to that compound. Hence compounds with higher RSC values elicited responses from a larger percentage of the receptors. This relationship implies strongly that the "taurine receptors" have a consistent and predictable specificity and thus appear to comprise a distinct receptor class. Regarding this specificity, no differences were observed between taurine sensitive receptors present on the lateral or the medial antennular filaments.

Additional tests of receptor specificity

In order to gain further insight into the restricted specificity of these cells, 12 α-amino acids, 3 organic acids, and the quaternary amine, glycine betaine, were tested at a concentration of 10^{-5} M on additional taurine sensitive receptors. Table III shows that individual compounds were applied to 5 to 65 receptors and that none of the new compounds cited above elicited responses. As in Tables I and II, the taurine analogs included in this test-series stimulated all receptors, whereas GABA and β-aminoisobutyric acid stimulated a large percentage of them. RSC values were not computed because in this phase of the study all of the compounds were not tested on all of the receptors. The inability of all α-amino acids to activate taurine sensitive receptors strongly supports the preceding results which indicated that amine groups in the *alpha* position reduced effectiveness. The ineffectiveness of the organic acids tested supports the earlier conclusion that stimulatory molecules require both positively and negatively charged atoms.

Quantitative effects of stimulatory compounds

Whereas the RSC values presented earlier for various compounds showed a consistent ranking with individual receptors, considerable variations were apparent

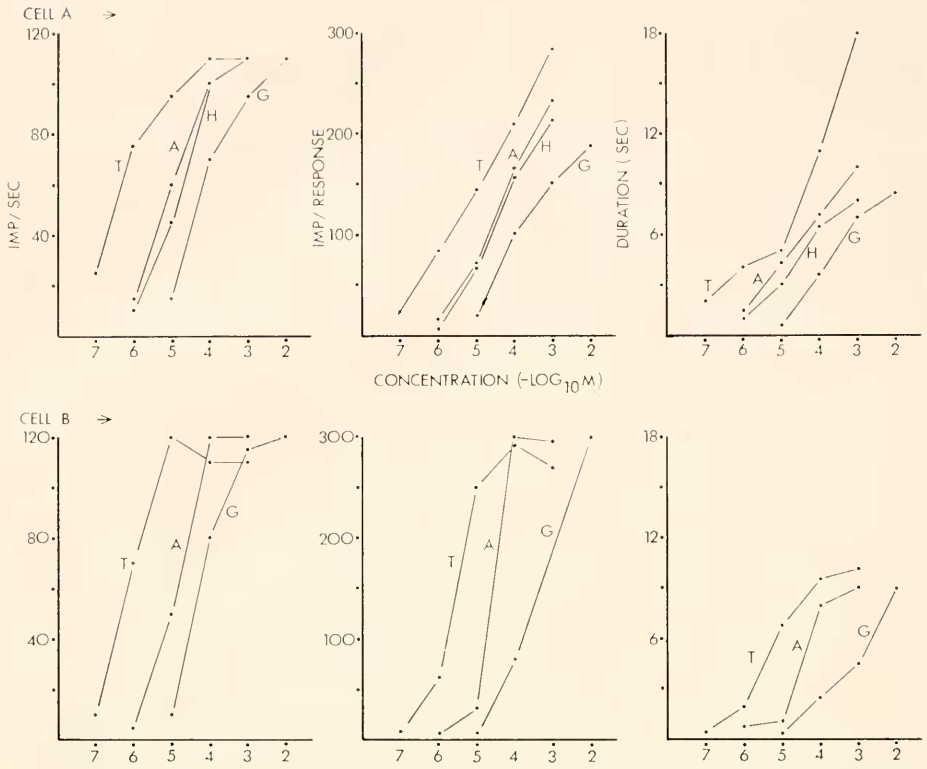

FIGURE 4. Three concentration-dependent response parameters (maximum impulse frequency, total impulses, and response duration) of two receptors stimulated with taurine (T), β-alanine (A), hypotaurine (H) and γ-amino-n-butyric (G).

in the RSC values obtained with individual compounds on different receptors. For example, β-alanine was usually the second more stimulatory compound, yet its RSC values ranged from 5 to 94 (Table I). To explore the basis of this variability, a detailed evaluation was made of three response parameters of two receptors tested with graded concentrations of the four most stimulatory compounds (Fig. 4). In both receptors, the concentration functions of the three parameters described a series of roughly parallel curves. Also in both receptors, maximum impulse frequency reached a maximum value and did not increase at higher concentrations. In the slower adapting receptor (Fig. 4A), impulses/response and response duration continued to increase with concentration; while in the more rapidly adapting receptor (Fig. 4B), these parameters reached maximum values at approximately the same concentration as frequency. This variation between the slow and fast adapting receptors likely results from the mode of stimulus introduction which was a pulse with an exponential dilution profile (see Fig. 1). Hence, as concentration increased, the period during which the pulse remained at a suprathreshold concentration also increased, thereby prolonging the response of the slow-adapting receptor.

In addition to the variations cited above, individual receptors also varied in sensitivity and in the profile of their dose-response curves. Note that the concentration function of impulses/response rises more sharply in the receptor represented in Figure 4B than that in Figure 4A. Individual variations in sensitivity indicate that response to the standard test concentration (10^{-5} M) will not occupy the same relative position on the dose-response curve of each receptor. In less sensitive receptors, a 10^{-5} M concentration of a given compound may be close to the threshold concentration. In very sensitive receptors, a 10^{-5} M concentration may be close to the plateau concentration. To return to the example of variation in the individual RSC values of β-alanine, it can be inferred that in a very sensitive, rapidly adapting receptor, the test concentration of 10^{-5} M may be near the plateau concentrations of both taurine and β-alanine, resulting in approximately equal RSC values. Conversely, in a less sensitive receptor, the test concentration may be near the threshold concentration of β-alanine, resulting in a very low RSC value. This inherent variability among receptors underscores the necessity of comparing RSC values only in cases where all compounds are applied to each receptor in the test population. These factors may also explain why GABA, the fourth most stimulatory compound, did not activate all receptors (Tables II and III). In less sensitive receptors, the test concentration may be below the threshold concentrations for GABA (see also Fig. 4).

That the three response parameters detailed in Figure 4A, B describe a series of roughly parallel curves suggests that these compounds effect impulse generation in

TABLE III

Sensitivity of taurine sensitive receptors to taurine analogs, α-amino acids and other compounds. All compounds were tested at 10^{-5} M.

Compound	Number of receptors tested	Number of receptors activated	Receptors activated (%)
L-α-Alanine	43	0	—
β-Alanine	33	33	100
α-Aminoisobutyric acid	8	0	—
β-Aminoisobutyric acid	8	5	63
γ-Amino-n-butyric acid	15	14	93
L-Aspartic Acid	30	0	—
Citric acid	10	0	—
L-Glutamic acid	19	0	—
Glycine	65	0	—
Glycine betaine	43	0	—
Hydroxy-L-proline	7	0	—
Hypotaurine	9	9	100
L-Isoleucine	7	0	—
L-Leucine	12	0	—
L-Lysine	8	0	—
Propionic acid	19	0	—
Succinic acid	19	0	—
Taurine	65	65	100
L-Tryptophan	7	0	—
L-Tyrosine	7	0	—
L-Valine	5	0	—

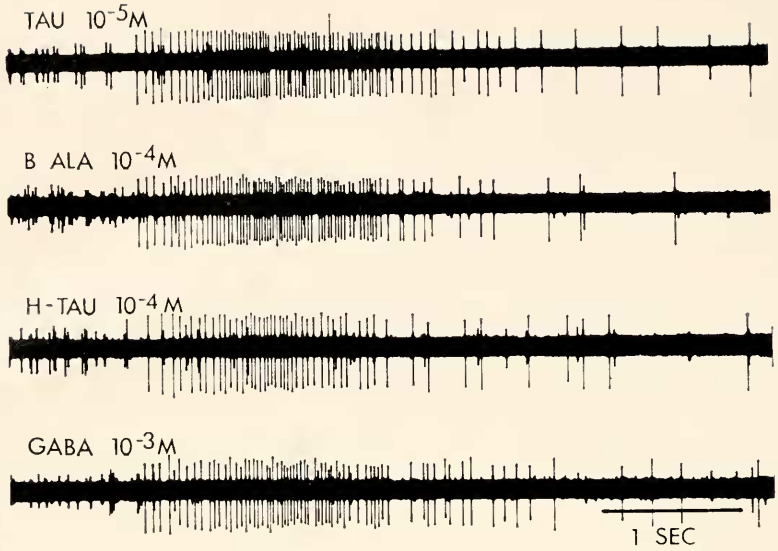

FIGURE 5. Response of single receptor to four stimulants with concentrations adjusted to elicit essentially equal-intensity responses. Time bar is 1 sec. Tau represents taurine; β-ala, β-alanine; H-Tau, hypotaurine; and GABA, γ-amino-n-butyric acid.

a manner mimicking the concentration function of a single compound. A less stimulatory compound effects receptor response in the same manner as a more stimulatory compound applied at a lower concentration. The functional implication is that the receptor response elicited by taurine at 10^{-5} M would be very similar to that of β-ala at 10^{-4} M and GABA at 10^{-3} M, as suggested by Figure 5.

DISCUSSION

These results indicate that the antennules of the spiny lobster, *Panulirus argus,* possess taurine sensitive receptors with a narrow and consistent response specificity. Previous electrophysiological studies of crustacean chemoreception indicate that individual receptors exhibit differential specificities to amino acids and related compounds (Laverack, 1964; Case, 1964; Ache, 1972; Shepheard, 1974; Fuzessery and Childress, 1975). The two studies dealing most thoroughly with receptor specificity (Case, 1964; Shepheard, 1974) provided values of the relative activity of compounds obtained by pooling results from the entire population of receptors tested. This practice treats all receptors as being effectively monotypic with respect to specificity. Moreover, in the above studies all compounds were not applied to each receptor in the test population. The latter procedure is essential for an analysis of both the specificity and the inherent variability of individual receptors. However, regarding the taurine sensitive receptors analyzed in the current study, some corroborating evidence is present in the study by Shepheard (1974) on another decapod crustacean, *Homarus americanus.* In a case in which 43

amino acids and related compounds were applied to a single receptor, only taurine and β-alanine were stimulatory.

It is important to emphasize that our current documentation of the distinct specificity of taurine receptors in *P. argus* was made possible largely by our early recognition of the extreme sensitivity of these receptors to taurine. This recognition led to our decision to work with a dilute (10^{-5} M) standard test concentration. As shown clearly in Figure 4, the apparent specificity of a receptor becomes less distinct as the test concentration is increased. The failure of earlier workers to detect receptor classes with distinct specificity in crustaceans may be due to using high stimulant concentrations (*ca.* 10^{-2} M).

Taurine sensitive receptors with a somewhat similar specificity to those found in antennules of *Panulirus argus* have been reported in endoreceptors serving a variety of functions. In the examples cited below, note that the activity of taurine was mimicked by the analogs hypotaurine and β-alanine but, in the instance where tested, not by the phosphonic acid analog. Also, in cases where tested, the taurine receptors were markedly less responsive to α-amino acids. Taurine is effective in suppressing induced heart seizures in dogs, and this action is most effectively mimicked by β-alanine, hypotaurine and GABA but not by glycine or α-alanine (Barbeau, Tsukada, and Inoue, 1976). Induced arrhythmia in dogs is suppressed by taurine but not by ethanesulfonic acid and other compounds lacking both basic and acidic groups (Welty, Read and Byington, 1976). In an active transport system in human blood platelets, taurine uptake is inhibited competitively by β-alanine and hypotaurine but not by the phosphonic acid analog (Grant and Nauss, 1976). Similarly, taurine uptake by rat brain slices is inhibited competitively by hypotaurine and β-alanine but not by α-amino acids (Kaczmarek and Davison, 1972; Lähdesmäki and Oja, 1973).

The inhibitory effect of GABA (= 4-aminobutyric acid) on crustacean stretch receptors is most effectively mimicked by 3 and 5 carbon chain amino acids with terminal amine groups, *i.e.*, β-alanine and 5-aminovaleric acid. 6-Aminocaproic acid was less effective, and glycine was essentially without effect. Taurine was less effective than its carboxylic acid analog, β-alanine (Robbins, 1959; Edwards and Kuffler, 1959). As in the present antennular system, the latter workers reported that the addition of neutral side chains reduced effectiveness, and that the presence of both the acidic and the basic groups were essential. In general, the GABA system appears to resemble the present one, differing primarily in that the ideal separation of opposite charges is three, rather than two, carbon atoms.

Similarities in the apparent specificity of both internal and external taurine receptors lend support to the concept that systems for molecular recognition, once evolved, may be preserved and used in a variety of functions, ranging from solute uptake and regulation to chemical sensing, synaptic transmission and others (Kittredge, Takahashi, Lindsey, and Lasker, 1974; Lenhoff, 1975). In the future we hope to provide a detailed model of the antennular receptor site for taurine. However, the presentation of such a model must await the testing of several additional analogs and derivatives that are not available commercially and hence must be specially synthesized.

Panulirus argus is a predator/scavenger that feeds on a variety of molluscs, arthropods, echinoderms and fish (Herrnkind, VanDerwalker and Barr, 1975).

Analyses of tissue extracts of marine molluscs, arthropods, echinoderms and fish show that the taurine concentration ranks from first to fifth in the total pool of free amino acids (Carr, 1976; Carr, Blumenthal and Netherton, 1977). Taurine is certainly the most abundant β-amino acid in most marine animals. According to Awapara (1976 p. 1), "taurine exists uncombined and distributed throughout the animal kingdom in a manner almost unparalleled by any known small organic molecule." Therefore, it is clear that taurine receptors could be expected to provide sensory information on the proximity of an array of suitable food organisms. Although the taurine analogs, hypotaurine and β-alanine, are also very stimulatory to the antennular taurine receptors, both of these compounds occur in only minor concentrations in the tissues of most organisms (Sturman, Hepner, Hofmann, and Thomas, 1976; Awapara, 1976). Hence, one must assume that the potential chemosensory role of these other stimulants is far less than that of taurine.

It is of special interest that taurine receptors are very insensitive to α-amino acids, particularly since these compounds are present in high concentration in the tissues of many marine animals. The antennular chemosensory system appears to be so constructed that a portion of the total receptor population responds to a single, ubiquitous β-amino acid, and is functionally insensitive to other commonly occurring amino acids. Perhaps the significance of this finding resides in the fact that α-amino acids are common constituents of sea water, occurring at individual concentrations of 10^{-7} to 10^{-9} M (Duursma, 1965). Comparable concentrations of taurine have not been reported. A plausible speculation may be that dissolved α-amino acids produce a chemical "white noise" against which chemosensory-based discrimination must occur. Taurine receptors would be unaffected by ambient α-amino acid levels, and therefore may provide less ambiguous information regarding the proximity of potential prey.

In the present antennular system, taurine appears to comply with Beets' (1971) definition of a nonideal mono-osmatic odorant, *i.e.*, a single compound which activates a single receptor at lower concentrations than other compounds within the specificity of that receptor. In addition, when one considers the chemical composition of the natural foods of *P. argus*, taurine is the only compound that we have tested which is likely to be present in sufficient concentrations to activate these receptors. From a functional standpoint, the antennular taurine receptors can be considered specialist receptors which may serve to monitor the presence of a single compound. This is particularly significant in that it is one of the few cases in which specialist receptors have been identified which may play a role in the mediation of feeding behavior, and the first documentation of such receptor organization in crustacean chemoreceptors.

Summary

1. Taurine sensitive receptors in the antennules of the spiny lobster, *Panulirus argus*, were identified electrophysiologically.

2. Recordings from single receptors revealed a narrow and consistent specificity when tested with taurine, taurine analogs and derivatives, and structurally related compounds.

3. Taurine was the most stimulatory compound tested. Threshold concentrations for 36 individual receptors ranged from 10^{-8} to 10^{-10} M.

4. The taurine analogs, hypotaurine and β-alanine, were also very effective but the phosphonic acid analog of taurine was ineffective.

5. Regarding receptor specificity, receptor stimulation was greatest with compounds having single terminal basic (amine) and acidic groups separated by two carbon atoms. Compounds having terminal basic and acidic groups separated by three to five carbon atoms were also active. However, activity decreased with the distance of separation of charged groups.

6. *Alpha*-amino acids and compounds with terminal basic and acidic groups separated by only one carbon atom were virtually ineffective.

7. Receptor stimulation was markedly less with structurally related compounds that either lacked a terminal amine group, had additional amine or acidic groups, or had neutral side chains.

8. Dose/response relationships of four differentially stimulatory compounds (taurine, hypotaurine, β-alanine and γ-aminobutyric acid) applied to single receptors were compared and found to describe a series of roughly parallel lines. This implies that a less stimulatory compound effects receptor response in the same manner as a more stimulatory compound applied at a lower concentration.

9. The possible role of taurine in food finding, and the similarity of the specificity of antennular taurine receptors and taurine endoreceptors identified in various organisms are discussed.

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